

A MONOGRAPH OF THE GENUS CONOPHOLIS (OROBANCHACEAE)¹

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The Orobanchaceae consist of about 15 genera, four of which are native to the conterminous United States. One of these, *Conopholis*, is the subject of this revision. Two of the remaining three, *Epifagus* and *Orobanche*, are sympatric with *Conopholis*. From these, *Conopholis* can be separated by its chasmogamous flowers—those of *Epifagus* being, in large part, cleistogamous—and by its exerted stamens—those of *Orobanche* being included.

Conopholis, a genus of plants parasitic upon the roots of *Quercus*, is confined to North and Central America and is composed of two major populations, one in eastern United States and adjacent Canada, and one in western United States, Mexico, and Central America. This bicentric pattern is found also in several other genera in North America, among them *Platanus*, *Juglans*, and *Liquidambar*.

Although five species of *Conopholis* have been described from different geographical areas, no comprehensive taxonomic study of the genus has been published. Uncertainty as to the number of species in the genus can be noted in standard works, e.g., Fernald (1950) accepted only one species, Beck-Mannagetta (1930) accepted two species, Small (1933) credited the genus with three species, and Gleason (1952) believed there to be four species. For these reasons, I felt the genus was in need of revision.

Unlike certain other members of the Orobanchaceae, *Conopholis* is of little or no economic importance. Although the plants are parasitic upon oaks, they seemingly do little harm to the host. Evidently no animal is known to feed upon the plants.

Conclusions presented in this thesis are based upon limited field study (in Florida, Georgia, Texas, and New Mexico) and upon a study of approximately 1350 herbarium specimens from the following 36 herbaria: ARIZ, ASC, AUA, C, DAO, DUKE, F, FSU, GA, GH, ILL, IND, KY, LAF, LL, MAINE, MEXU, MICH, MO, NEBC, NHA, NY, OS, PAC, PH, SMU, TAES, TEX, UC, UNM, US, VDB, VPI, VT, WIS, and WVA (abbreviations according to Lanjouw and Stafleu, 1964). In order to conserve space, a list of specimens examined is not included in this paper. I shall be happy to send a mimeographed copy of exsiccata to anyone who requests it.

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REVIEW OF LITERATURE

The genus *Conopholis*, established by Wallroth (1825), was based upon a Linnaean species, *Orobanche americana*, described in 1767. Since that time four other specific names have been added to the genus. Liebmann (1847) described two species from Mexico, *C. alpina* and *C. sylvatica*. *Conopholis alpina*, described from Chinautla, District Tinzutlan, Puebla, was said to be distinguishable from *C. americana* by its calyx being unibracteolate, divided anteriorly almost to the base, and not divided posteriorly; by its corolla being twice as long as the calyx, with its upper lip reflexed and entire, and the lobes of the upper lip not longer than the lower lip, and with the lobes of the lower lip short, lanceolate, and entire; by its stamens being much exserted; by its style being angular, reflexed, and hardly longer than the stamens; and by its capsule being apiculate (not having a long curved beak) and shorter than the bracts. *Conopholis sylvatica*, described from Totutla and the Hacienda de Mirador, Veracruz, was said to differ from *C. americana* by its slenderer stem; by its smaller calyx being split to the middle anteriorly and bidentate posteriorly; and by its slenderer corolla being twice as long as the calyx, the lobes of the lower lip being shorter and more obtuse.

Watson (1883) described *C. mexicana* from the Sierra Madre, south of Saltillo, and from Soledad, Coahuila. It was said to be distinguishable from *C. americana* by its longer and more rigid lanceolate acuminate scales, by its less deeply toothed calyx, and by its larger corolla.

Finally, *C. panamensis* was described by Woodson (Woodson and Seibert, 1938) from Chiriquí, Panama. It was said to be distinguishable from both *C. americana* and *C. mexicana* by its barely bilabiate calyx with rather shallow, broadly obtuse lobes.

Wilson (1898) studied *C. americana* morphologically and anatomically. Although her paper is one of the major sources of vegetative anatomical data on the genus, it is sadly lacking in depth. It covers many facets of the genus but goes into detail on none. Doak (1929) gave additional data on the structure of the gall.

Percival (1931) studied *C. americana* to determine the nature and development of the connection between the parasite and its host. He included several anatomical and morphological features of the species, as well as some ecological data.

A detailed study of seed development in *C. americana* was made by B. Tiagi (1965). He pointed out several seed and embryological characters unique in the Orobanchaceae to *Conopholis*.

Nelson (1919), Clute (1919), and Jennings (1920) published brief notes concerning the rarity of *Conopholis* in parts of northeastern United States.

MORPHOLOGY

Habit. The *Conopholis* plant consists of several to many erect flowering stalks and buds arising from a gall on an oak root. The gall is produced by

the root as a result of the presence of the parasite. Although roots are occasionally found to extend past the gall, the parasite normally prevents further growth of the root. The duration of the flowering stalk is undoubtedly annual, but according to Wilson (1898) and to my observation (of dead and living flowering stalks on the same gall at the beginning of the growing season), the gall is certainly perennial. Wilson suggested that the gall probably lives 4 to 5 years before any flowering stalks are produced. The duration of the buds is not known. They may remain dormant for 1 year or may be capable of rapid growth, maturing in one growing season.

Gall. The gall ("tubercle") is covered by a thick, coarse, porous, dark-brown bark and is composed of "innumerable granules of sclerenchyma" (Wilson, 1898). The *Conopholis* seed germinates in the soil near a young oak root (Percival, 1931). The young seedling parasitizes the oak root, causing it to produce massive amounts of tissue, thus forming the gall (Wilson, 1898). According to Doak (1920) and to Percival (1931), however, the gall is made up largely of *Conopholis* tissue. *Conopholis* flowering shoots are initiated within the gall, eventually breaking through its thick bark. Galls have been found ranging from 0.5 to 10 inches in diameter (Wilson, 1898; Boeshore, 1920).

Stem. The stem is erect, typically unbranched, usually terete, strongly grooved, and glabrous to slightly glandular pubescent. I have seen only one specimen with a branched stem: Kentucky, Bullitt Co., *Gunn 616*, 16 May 1966 (KY).

Leaves. The leaves, reduced to scales, are simple, sessile, exstipulate, and, at first, cream-colored but later turning brown and membranous. The lowest portion of the stem is densely covered with crowded leaves, while just above the stem base the leaves become more distant and much larger. Although they vary much in length and width, the upper leaves are taxonomically useful, usually maintaining, within a species, a fairly constant length:width ratio and a uniform shape and texture. The leaves may bear stalked or sessile glands or they may rarely be glabrous.

Inflorescence. The inflorescence is a crowded raceme composed of imbricate bracts, each subtending a flower. The denseness and thickness of the inflorescence are usually good taxonomic characters.

Bracts. Each flower is subtended by one bract that greatly resembles the leaves. The bracts are probably the structures most useful taxonomically. In *C. americana*, for example, the bract nearly or wholly surrounds the base of the flower, is usually very thin in texture, and maintains a low length:width ratio.

Flowers. The flowers are sympetalous, zygomorphic, perfect, and cream-colored and usually have one or two bractlets arising on the base of the calyx.

Calyx. The calyx is the most variable part of the plant. It is tubular and has acute to rounded teeth or lobes. Some *Conopholis* species have been

described on the basis of calyx differences, but due to great variability, these differences cannot alone be used as criteria of taxonomic value. One or two bractlets arise on the base of the calyx.

Corolla. The corolla is tubular, sometimes reflexed distally, and two-lipped, with the upper lip external in the bud and notched or rarely three- to four-lobed, and the lower lip usually three-lobed, or rarely one- or two-lobed. The corolla persists for a while around the maturing capsule but eventually is split by the enlarging capsule and falls off. Corolla length is a good taxonomic character.

Androecium. Four stamens, all fertile, the lateral two sometimes connate, are usually present in each flower. Gray (1888) reported that a fifth stamen is occasionally present. My observations have not confirmed the presence of a fifth stamen. The stamens are epipetalous, arising on the corolla tube at a level just above the summit of the ovary, and are well exerted. The reflexed tip of each filament bears an anther with two thecae that dehisce longitudinally. The thecae of the anther are slightly divergent, basally attenuate, and glabrous to sparingly pilose.

Gynoecium. The gynoecium is superior, irregularly shaped, compound, four-carpellate, multiovulate, and unilocular. Traditionally the gynoecium of many Orobanchaceae, including *Conopholis*, has been interpreted as having two median carpels, each carpel bearing two placentae, these being displaced from the margin towards the median line of the carpel. According to this interpretation, each of the resulting four parietal placentae is the product of only one carpel. In contrast, Y. D. Tiagi (1962) interpreted the gynoecium of these Orobanchaceae as having *four* carpels, two median and two lateral, each carpel bearing two marginal placentae. According to him, the placentae of adjacent carpels are fused, and thus the ovary contains four parietal placentae, each placenta being the product of *two* carpels. I am accepting Tiagi's interpretation. The four carpels of *Conopholis* are equal; however, there is a deep groove over the midrib of the median carpels, and the lateral carpels lack midrib bundles (Y. D. Tiagi, personal correspondence). The ovules of *Conopholis* may be stalked or sessile and are variously shaped. This variation results from pressure exerted by the enlarging ovules. The pressure frequently results in their partial or complete fusion in pairs (B. Tiagi, 1965). Usually the ovules become inverted, but some, due to crowding, do not fully invert. The stigma is either depressed centrally or horizontally furrowed and is capitate on a long style that is often apically reflexed.

Fruit. The fruit of *Conopholis* is a two-valved, single-celled, many-seeded, dark brown to black capsule. According to B. Tiagi (1965), the capsule dehisces anteroposteriorly along the grooves that lie in line with midrib bundles of the median carpels. My observations indicate that dehiscence also may be irregular.

Seeds. The seeds of *Conopholis* are large relative to those of other Orobanchaceae. They are variously shaped: oval, triangular, quadrangular,

or rhomboidal in outline, with rounded, or less often, sharp angles. The various shapes are due to the pressure exerted by the enlarging ovules (B. Tiagi, 1965). According to Martin (1946) the seeds of *Conopholis* are microembryonic, containing a small oval embryo surrounded by a massive endosperm. The color of the seeds varies from light to dark brown, with the testa usually being marked with darker brown to black lines forming a reticulum. The seeds are not taxonomically important because of their great variability.

CYTOLOGY AND ANATOMY

Chromosome number. The only report of a chromosome number for *Conopholis* is that of Lewis (1966), $n=20 (\pm 1)$ for *C. americana*, the eastern species. My attempts to make chromosome counts of western *Conopholis* from root tip smears were unsuccessful due to failure to obtain seed germination.

Embryology. That *Conopholis* has several embryonic characters elsewhere unknown in the Orobanchaceae was shown by B. Tiagi (1965). Some of these are as follows.

The massive integument is composed mostly of about nine layers of cells; however, towards the funicle and chalaza it consists of more than 12 cell layers.

The nucellus is single-layered and ephemeral, disappearing by the time the embryo sac matures. As the nucellus degenerates, two or three layers of the integument surrounding the embryo become glandular. This tissue, consisting of uninucleate vacuolated cells, acts as the endothelium. In most Orobanchaceae, the endothelium is composed of a single cell layer; therefore, the well developed massive endothelial tissue is a remarkable feature of *Conopholis*.

In the seed the endothelium cells, after serving a nutritive function, become extremely thickened due to the deposition of hemicellulose, which may serve as an additional source of food for the embryo. Probably for this reason and also because the endosperm is surrounded by this protective coat of endothelium, the peripheral cells of the endosperm do not develop a cuticle. Without an intervening cuticle, they can then absorb nourishment directly from the endothelium at the time of germination.

Epidermal cells. The epidermal cells of the leaves of *Conopholis* are highly lignified and have thick, extremely pitted walls. Wilson (1898) reported that stomates are absent on the leaves of *Conopholis* but are present on the flowering stalk, but Boeshore (1920) found some misshapen and poorly developed stomates on the outer surface of the upper leaves. These appeared to be functionless or nearly so. Some had two elongated guard cells which had "slipped out of position" and showed a long orifice between them, while others had three or four loosely fitted guard cells. I have made but few slides of epidermal tissue. These have not contained any recognizable stomates or guard cells.

ECOLOGY

Habitat. *Conopholis* occurs under oak trees in moist mixed or deciduous forests, oak woodlands, and mixed montane forests. The number of plants parasitizing a host may vary from one to many, the latter forming almost matlike growths up to 20 feet across.

Pollination. Thus far, I have observed only one insect visiting a *Conopholis* flower, a bumblebee on *C. americana*, the eastern species: Georgia, Grady Co., Haynes 2679, 11 April 1968 (DUKE, GH, LAF, VDB). I have seen only one other specimen with insect visitation data: P. S. Martin observed bumblebees visiting *C. alpina* var. *alpina* flowers in central Mexico: Tamaulipas, Martin 56, 10 March 1953 (MICH).

I have found dehisced anthers in flower buds of herbarium specimens and of plants preserved in 50% methanol. A slide of pollen from dehisced anthers of a flower bud from a methanol-preserved plant revealed that about one-half of the pollen grains already had germinated. Perhaps *Conopholis* is not obligately insect pollinated but is, at least occasionally, self pollinated in the bud.

Parasitism. The question arises concerning the generic host-specificity of *Conopholis*. Is *Quercus* the sole host, or are plants of other genera parasitized? I have seen *Conopholis* specimens with data indicating that the plants grew under *Fagus*, *Pinus*, *Juniperus*, *Acer*, *Ulmus*, *Cornus*, *Juglans*, *Carya*, *Liquidambar*, or *Cupressus*. I myself have found *Conopholis* under *Tilia* and *Pinus*, but after digging up the parasitized root, I found that it would always lead to a *Quercus*. I believe that if the collectors of the specimens whose data suggest a non-*Quercus* host would have done the same, they would have found the host actually to be *Quercus*. Wilson (1898) and Boeshore (1920) both concluded that *Quercus* is the sole host.

According to literature and herbarium-label data, *Conopholis* parasitizes the following hosts: (1) *Conopholis americana*: *Quercus alba*, *Q. bicolor*, *Q. borealis*, *Q. falcata*, *Q. hemisphaerica*, *Q. marilandica*, *Q. nigra*, *Q. petrea* (cultivated in Copenhagen, Denmark), *Q. shumardii*, *Q. velutina*, and "Chestnut oak"; and (2) *Conopholis alpina*: *Q. gambellii*, *Q. grisea*, *Q. texana*, *Q. utahensis*, and "Grey oak."

SYSTEMATIC TREATMENT

Five species of *Conopholis* have been described. However, the characters used to distinguish most of these are too variable to be significant taxonomically. I am recognizing but two species, one of them being divided into two varieties. These three taxa could perhaps have been treated as varieties of one species, but because of the reproductive isolation, the morphological distinctness, and the apparent host-specificity of the eastern and western populations, I prefer to treat them as two species.

The two species of *Conopholis* are allopatric. The range of *C. americana* is limited to the United States east of the Mississippi River and to southeastern Canada, whereas *C. alpina* is restricted to southwestern United

States, Mexico, and Central America. So far as is known, the two species approach no closer than about 800 miles to each other (Fig. 4, 5).

A possible explanation for the disjunct range of plants with a distribution similar to *Conopholis* is offered by Sharp (1966). He postulates that much of the present Mexican vegetation had its origin in the circumboreal flora that existed in northern Asia and northern North America during the Cretaceous. Many species of this flora [probably including *Conopholis*] migrated southward into the United States and Mexico during the Cretaceous and Tertiary. The rigorous climate of the Tertiary and Pleistocene subsequently extinguished most of them throughout North America. A few survived in the southeastern United States and many more in Mexico and Central America.

The two species of *Conopholis* are morphologically distinct. No single character can be relied upon to determine all specimens encountered, but when several characters are collectively considered, a specimen in question can easily be referred to the correct taxon. At a glance I was able to determine to species 90% of all *Conopholis* specimens seen by me. After examining the remaining specimens with a microscope, I had no problem determining them.

So far as is known, the host plants are different species of *Quercus*. Apparently only two of the many North American oaks occur sympatrically with both species of *Conopholis*. These are *Q. virginiana* and *Q. muhlenbergii*, neither of which is known to be a host of *Conopholis*. Possibly one of the species could parasitize the hosts of the other, but such a condition has yet to be demonstrated.

Much cytological, anatomical, and biochemical work needs to be done on the genus. Then perhaps the monographer will see a need to consider the various taxa as varieties of one species, but hopefully this work will support my conclusions.

CONOPHOLIS Wallroth, Orob. Gen. Diask. 78. 1825.

Low, glabrous or sparsely to densely glandular-pubescent, cream, yellow-brown, brown, or black simple or rarely branched herbs, fleshy at first but becoming brittle, the flowering stems arising from a dark brown to black gall. Leaves scale-like, sessile, with invisible to plainly evident veins, fleshy at first but becoming brittle, of 2 types, the lower very tightly imbricate, short, and wide, the upper larger, scattered to somewhat imbricate, and alternate. Inflorescence a compact raceme, each flower axillary to a sessile bract, the pedicels very short to elongate, the bracts longer than the calyx. Calyx tubular, 2-lipped, split anteriorly, 2- or 4- to 5-toothed or -lobed, the divisions broadly to narrowly acute or rounded; 1 or 2 subulate bractlets may arise on the base of the calyx, or these may be absent. Corolla cream-colored, tubular, sometimes reflexed apically, 2-lipped, the upper lip rounded, notched, rarely 3- or 4-lobed, external in the bud, the lower lip 3-lobed, or rarely 1- or 2-lobed, the lobes rounded to acute;

corolla somewhat persistent, eventually ruptured and dislodged by the enlarging capsule. Stamens 4 (-5?), the lateral 2 sometimes connate, epipetalous, inserted above the ovary; the filaments elongate; anthers free, exerted, thecae somewhat divergent, basally attenuate, glabrous to sparingly pilose; pollen grains triaperturate. Style apically reflexed, included or exerted, persistent on or deciduous from the fruit; stigma capitate, slightly depressed centrally to horizontally furrowed. Fruit a 2-valved, single-celled, dull dark brown to black capsule dehiscing irregularly or anteroposteriorly. Seeds oval, triangular, quadrangular, or rhomboidal with rounded or, less often, sharp angles, light brown to dark brown, with brown to black lines forming a reticulum. (Name from the Greek *conos*, cone and *pholis*, scale.)

Type species. Conopholis americana (Linnaeus) Wallroth (*Orobanche americana* Linnaeus).

KEY TO THE TAXA

1. Plants of eastern United States and Canada; scale length:width ratio 1.5-2.3 (3); bract length:width ratio 1.6-2.5 (3.3); inflorescence loose, 13-28 mm thick; fruit mostly with the style persistent; plant glabrous to slightly pubescent; corolla not over 14 mm long, mostly not reflexed; bracts nearly or wholly concealing the calyx; anthers glabrous.
 1. *C. americana*
1. Plants of western United States, Mexico, and Central America; scale length:width ratio 2.4-4.2; bract length:width ratio 3-5.2; inflorescence mostly compact, (20) 28-40 mm thick; fruit mostly with the style deciduous; plant glabrous to densely glandular pubescent; corolla to 20 mm long, mostly much reflexed; bracts sometimes concealing the calyx, sometimes not; anthers often sparingly pilose 2.
2. Plants of southern Mexico and Central America; scales membranous, the veins slightly visible to plain; corolla 7.5-13.5 mm long; plant glabrous; bracts nearly or wholly concealing the calyx; calyx lobes often rounded, 0.3-1.6 mm long 2a. *C. alpina* var. *alpina*
2. Plants of western United States and northern Mexico; scales firm, the veins invisible; corolla (10.5) 14-20 mm long; plant glandular pubescent, at least along margins of scales and calyx lobes; bracts not concealing the calyx; calyx lobes sharply acute, (0.5) 1.5-4 mm long.
 2b. *C. alpina* var. *mexicana*

1. CONOPHOLIS AMERICANA (Linnaeus) Wallroth, Orob. Gen. Diask. 78. 1825.

Orobanche americana Linnaeus Mant. Pl. 88. 1767.

Stems erect, simple or rarely branched, glabrous, 6-20 (27) cm high, 4-12 mm in diameter. Leaves glabrous, with sessile glands, or rarely minutely glandular pubescent along the margins, broadly to narrowly lanceolate or elongate triangular, 5.5-18 (21) mm long, 4.5-12 mm wide, widest at or just above the base, apex acute to nearly rounded; veins obscure to slightly visible. Bracts glabrous or rarely minutely pubescent along the margins,

broadly to narrowly lanceolate or elongate triangular, often nearly or wholly concealing the calyx, 5.5-18 mm long, 2-8 mm wide. Calyx irregularly 4- to 5-toothed or -lobed, the tube more or less cylindric, 3.3-8 mm long, split anteriorly from half-way to nearly to the base, the teeth or lobes acute, 0.5-3 mm long; bractlets two, 2.5-12 mm long. Corolla 8-14 mm long. Filaments 6-10.5 mm long; anthers glabrous, 1.5-2.3 mm long. Capsule mostly with the style and stigma persistent, 5-13 mm long, 5.5-11 mm in diameter. Seeds 0.5-1.5 mm long, 0.5-1.2 mm wide, and 0.4-0.7 mm thick. Figure 1.

Under oaks in moist, deciduous or mixed woods from Nova Scotia to western Wisconsin and south to Florida. Flowers from mid-February in the south to mid-June in the north.

Holotype: U.S.A. "CAROLINA": Garden (*Linn. Herb.* 798.5) (LINN). Figure 6.

2a. *CONOPHOLIS ALPINA* Liebmann var. *ALPINA*, Forh. Skand. Naturf. Möde 4: 184. 1847.

Conopholis panamensis Woodson, Ann. Missouri Bot. Gard. 25: 835. 1935.

Conopholis sylvatica Liebmann, Forh. Skand. Naturf. Möde 4: 185. 1847.

Stems erect, simple, glabrous, 8-28 cm high, 6-10 mm in diameter. Leaves glabrous, lanceolate to narrowly elongate triangular, (7) 12-21 mm long, 3-7 (11) mm wide, widest at or just above the base, apex usually sharply acute; veins slightly visible to prominent. Bracts glabrous, lanceolate to narrowly elongate triangular, often concealing the calyx, 10-20 mm long, 4-6 mm wide. Calyx irregularly 2- or 4- to 5-toothed or -lobed, the tube more or less cylindric, 3.3-4.5 mm long, split anteriorly from about half-way to all the way to the base, or not split at all, the teeth or lobes acute, to rounded, 0.3-1.6 mm long; bractlets 1 or 2 or absent, 2-4.5 mm long. Corolla 7.5-15.5 mm long. Filaments 9-12.5 mm long; anthers glabrous, rarely sparingly pilose, 1.6-2 mm long. Style and stigma 5.5-8 mm long. Capsule mostly with the style and stigma deciduous, 8-16 mm long, 5-11 mm in diameter. Seeds 0.4-1.7 mm long, 0.3-1.2 mm wide, and 0.3-0.8 mm thick. Figure 2.

Under oaks in montane forests, southwestern Tamaulipas south to Michoacan, Mexico and Chiriquí, Panama. Flowering from mid-December to late April.

Lectotype: MEXICO. PUEBLA: In rupibus Tepeyecuapa pr. Chinaulta ad radices Pinorum. Alt. 8600 ft. *Liebmann* 3719, March 1841 (C). Isotype: F. In the original description Liebmann referred to two collections. He did not designate either one as the type; therefore, I am herein designating one as the lectotype. Figure 7.

After examining the type specimens of *C. alpina*, *C. sylvatica*, and *C. panamensis*, I concluded that all are plants of the same species. The names *C. alpina* and *C. sylvatica*, described in the same publication, have 88 years priority over *C. panamensis*. Following article 57 (Lanjouw, 1966) I have chosen *C. alpina* as the specific name.

2b. *CONOPHOLIS ALPINA* Liebmann var. *MEXICANA* (Gray ex Watson) Haynes, *Sida* 3: 347. 1969.

Conopholis americana sensu Endlicher *Iconogr.* t. 81. 1838.

Conopholis mexicana Gray ex Watson, *Proc. Amer. Acad. Arts & Sci.* 18: 131. 1883.

Stems erect, simple, glabrous, 11-33 cm high, 5-12 mm in diameter. Leaves mostly quite glandular pubescent, rarely so only along the margins, narrowly lanceolate or narrowly elongate triangular, (7) 12-22 mm long, 3-9 mm wide, widest at or just above the base, apex mostly acute, rarely rounded; veins usually invisible. Bracts mostly quite glandular pubescent, rarely so only along the margins, narrowly lanceolate or narrowly elongate triangular, mostly not concealing the calyx, 12-22 mm long, 1.5-7 mm wide. Calyx irregularly 4- to 5-toothed or -lobed, the tube more or less cylindrical, (3.5) 6-9 mm long, split anteriorly from about half-way to all the way to the base, or not split at all, the teeth or lobes acute, (0.5) 1.5-4 mm long; bractlets 1 or 2 or absent, (0.8) 2-6.7 mm long. Corolla (10.5) 14-20 mm long. Filaments 7-12 mm long; anthers mostly sparingly pilose, 1.5-2.5 mm long. Style and stigma 5-12 mm long. Capsule mostly with the style and stigma deciduous, 8-15 mm long, 6-12 mm in diameter. Seeds 0.5-1.3 mm long, 0.5-1 mm wide, and 0.4-0.8 mm thick. Figure 3.

Under oaks in oak woodlands and mixed montane forests, Trans-Pecos Texas to northern New Mexico and central Arizona, south to central Oaxaca. Flowering from mid-February to late July, rarely to September.

Holotype: MEXICO. COAHUILA: Sierra Madre, 40 miles south of Saltillo. *Palmer 996*, March 1880 (GH). Isotypes: F, NY, PH, US, VT. Figure 8.

Over most of its range this variety is easily distinguishable from var. *alpina*. In areas of overlap, however, some specimens cannot confidently be placed into either taxon. For this reason I consider these two taxa to be varieties of one species.

Variety *mexicana* occurs sympatrically with var. *alpina* only in the southernmost part of its range. In this area it can generally be distinguished from var. *alpina* by the veins of its leaves and bracts being invisible, by its bracts mostly not concealing the calyx, and by its pubescence being mostly glandular.

EXCLUDED SPECIES

Conopholis ludoviciana Wood, *Class-Book Bot.* 512. 1867. = *Orobanche ludoviciana* L.

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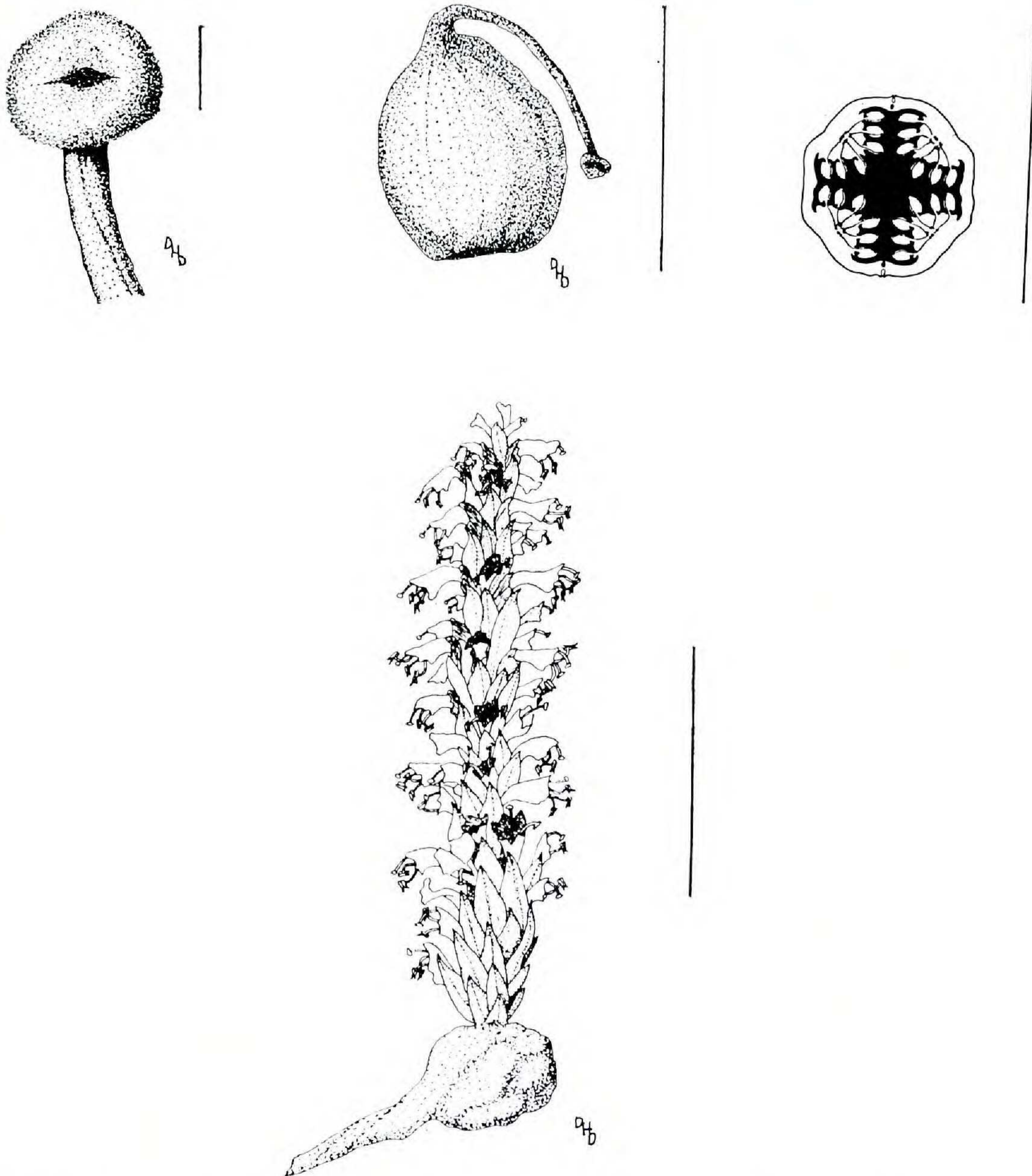


Fig. 1. *Conopholis americana*. Stigma (upper left), the vertical line represents 0.1 cm. Fruit (upper center), cross-section of ovary (upper right), the vertical lines represent 1 cm. Habit sketch (lower), the vertical line represents 5 cm.

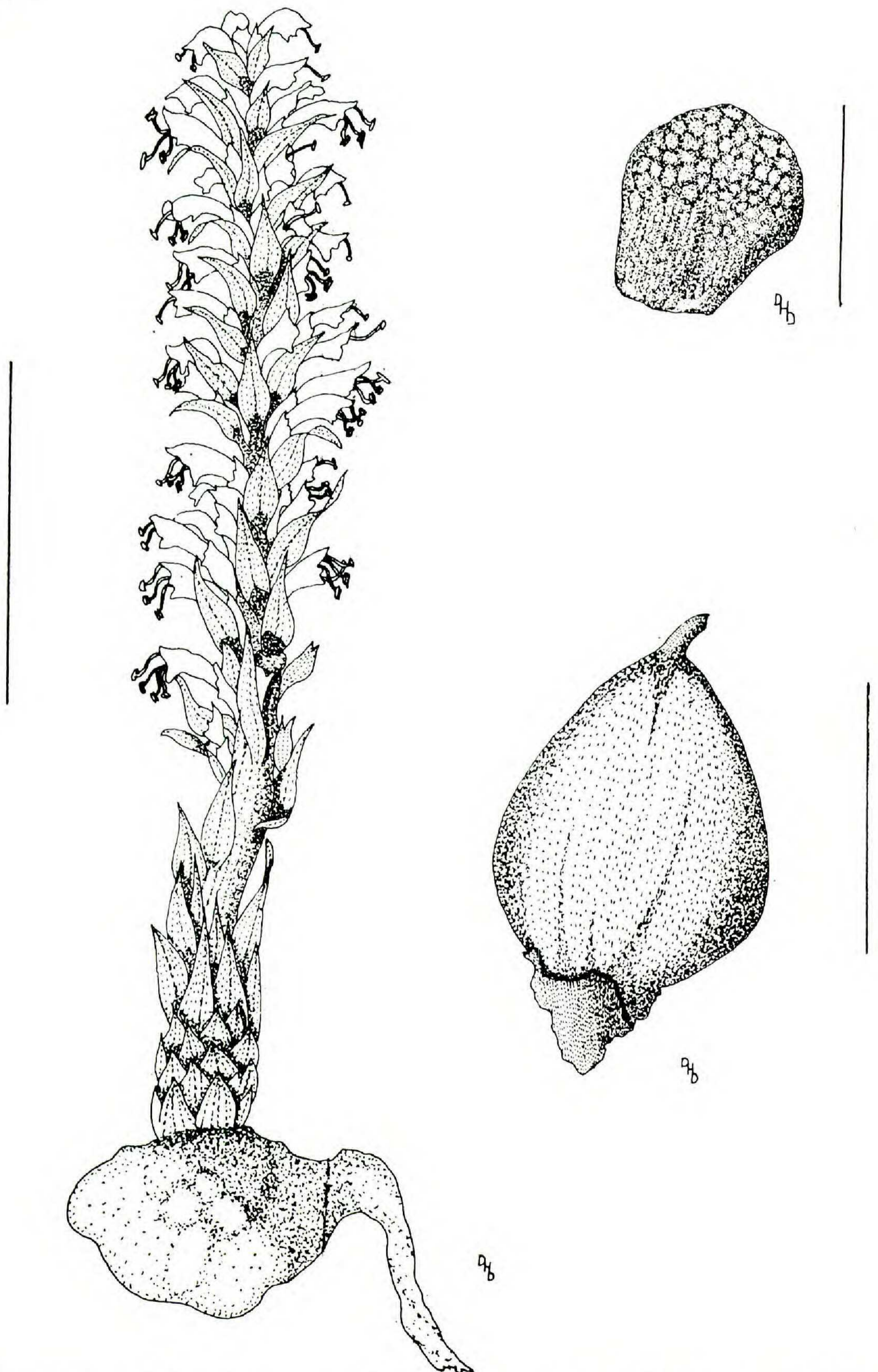


Fig. 2. *Conopholis alpina* var. *alpina*. Habit sketch (left), the vertical line represents 5 cm. Seed (upper right), the vertical line represents 0.1 cm. Fruit (lower right), the vertical line represents 1 cm.

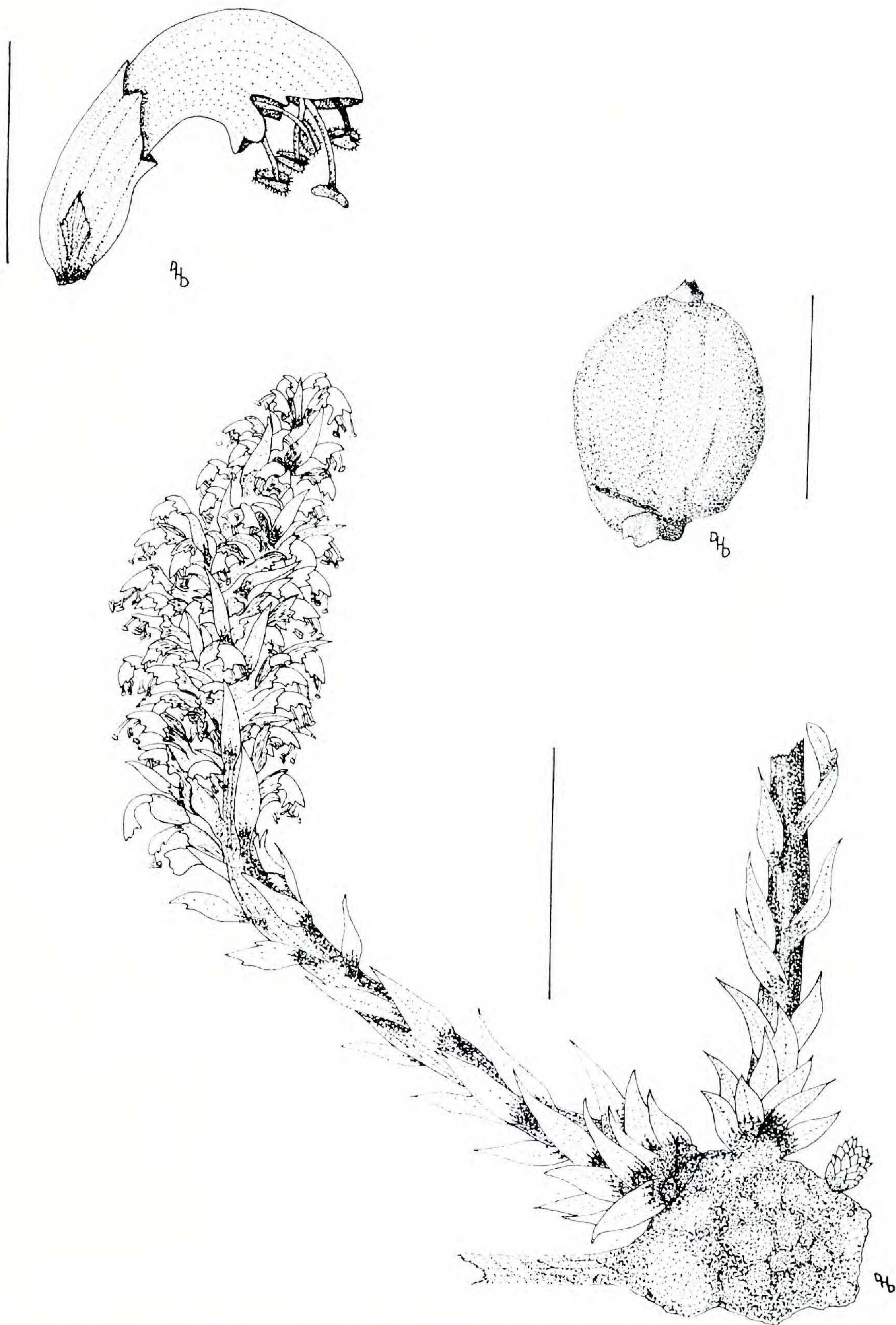


Fig. 3. *Conopholis alpina* var. *mexicana*. Flower (upper left), fruit (upper right), the vertical lines represent 1 cm. Habit sketch (lower), the vertical line represents 5 cm.

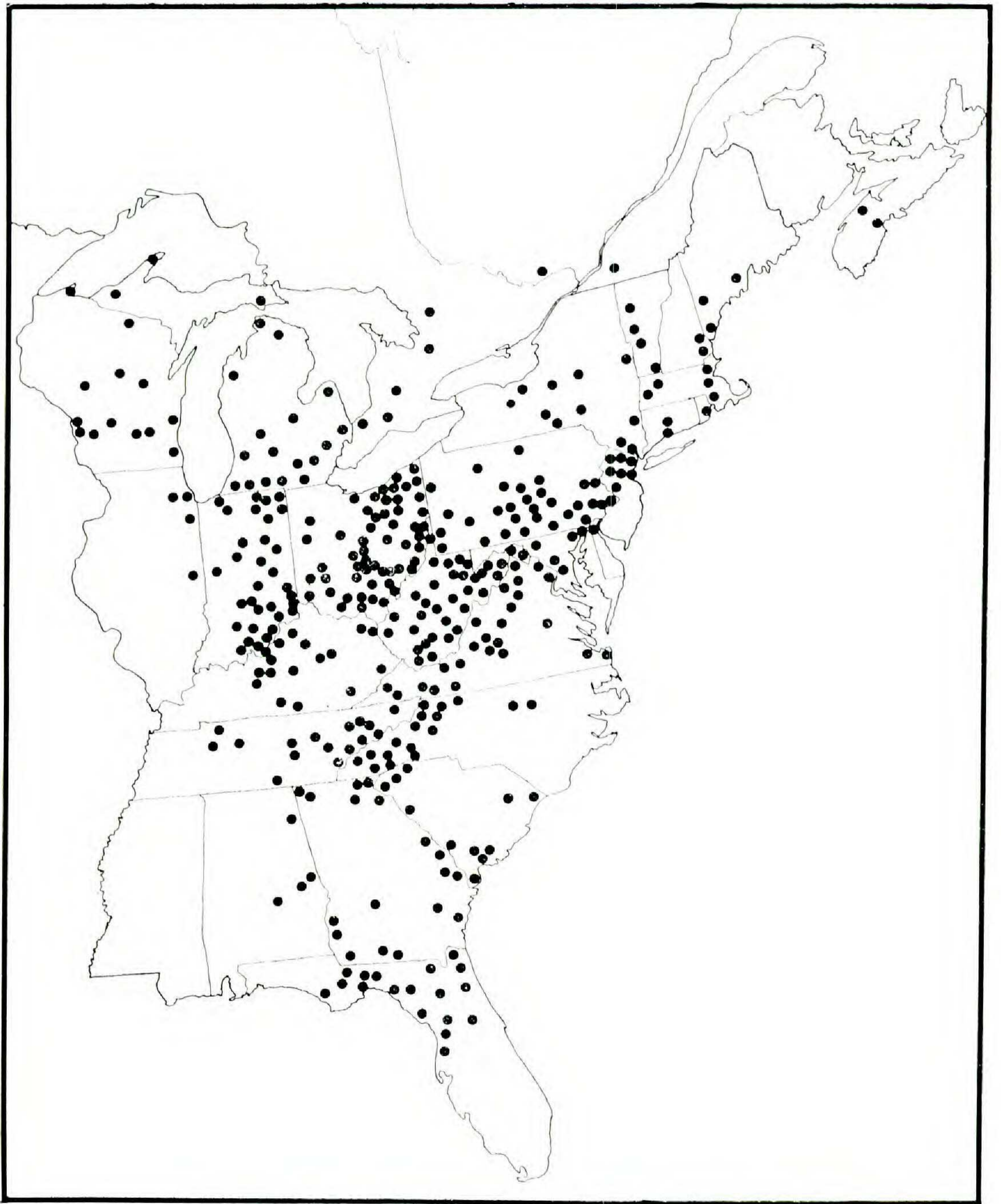


Fig. 4. *Conopholis americana*. Documented distribution.

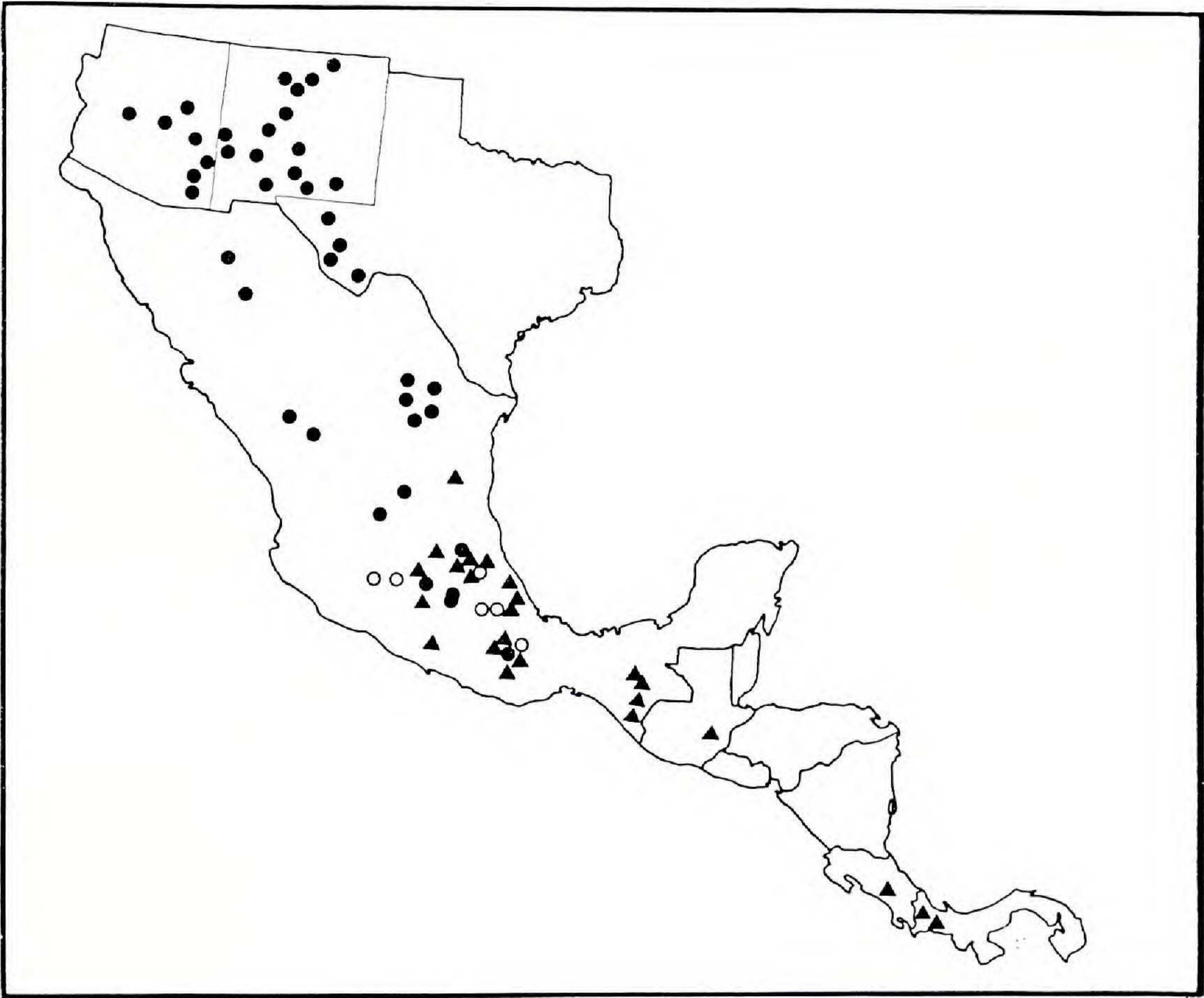


Fig. 5. *Conopholis alpina*. Documented distribution. *C. alpina* var. *alpina* (triangle); *C. alpina* var. *mexicana* (closed circle); *C. alpina*, specimens that could not be determined to variety (open circle).

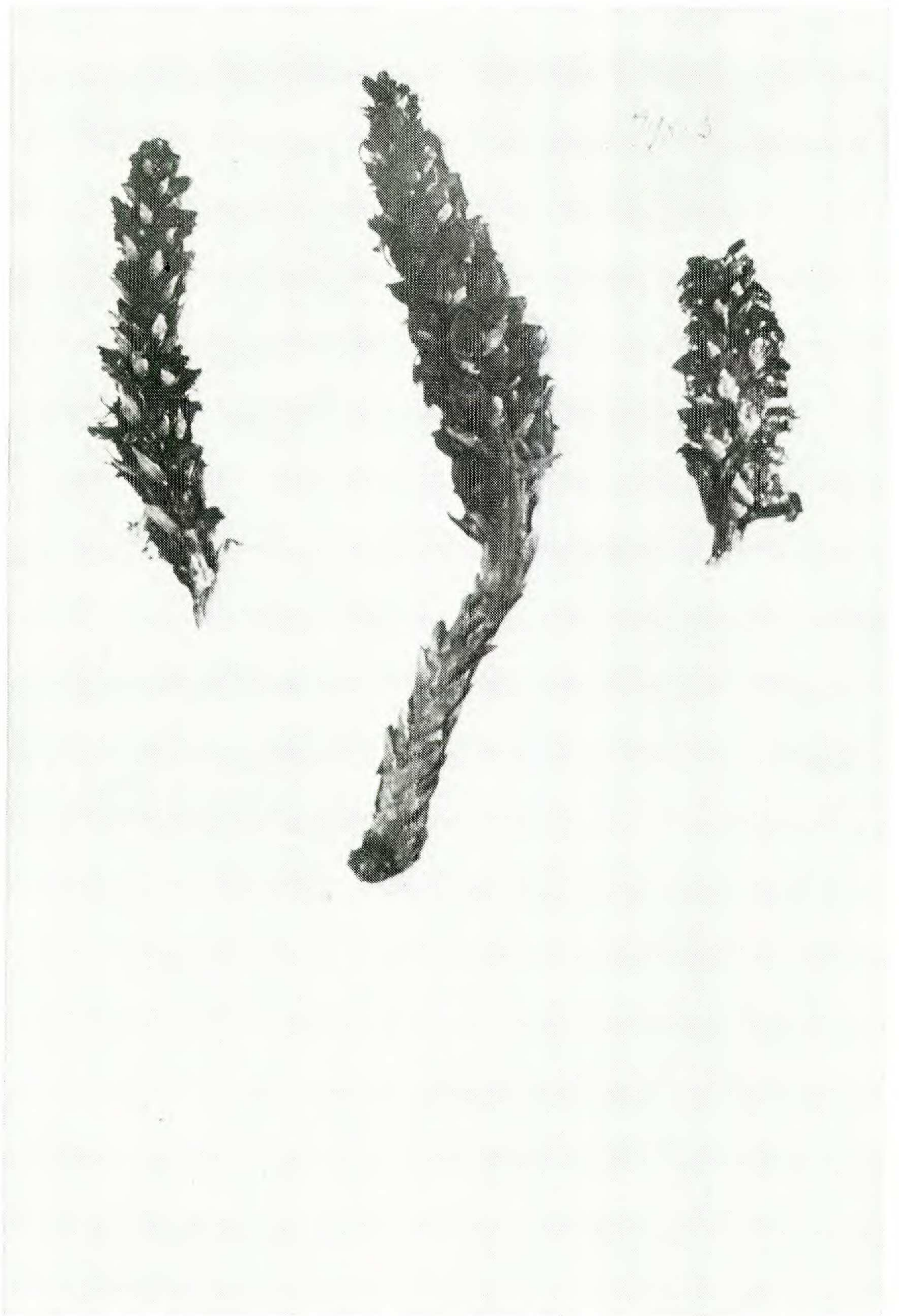


Fig. 6. *Conopholis americana*. Photograph of holotype.



Fig. 7. *Conopholis alpina* var. *alpina*. Photograph of lectotype.

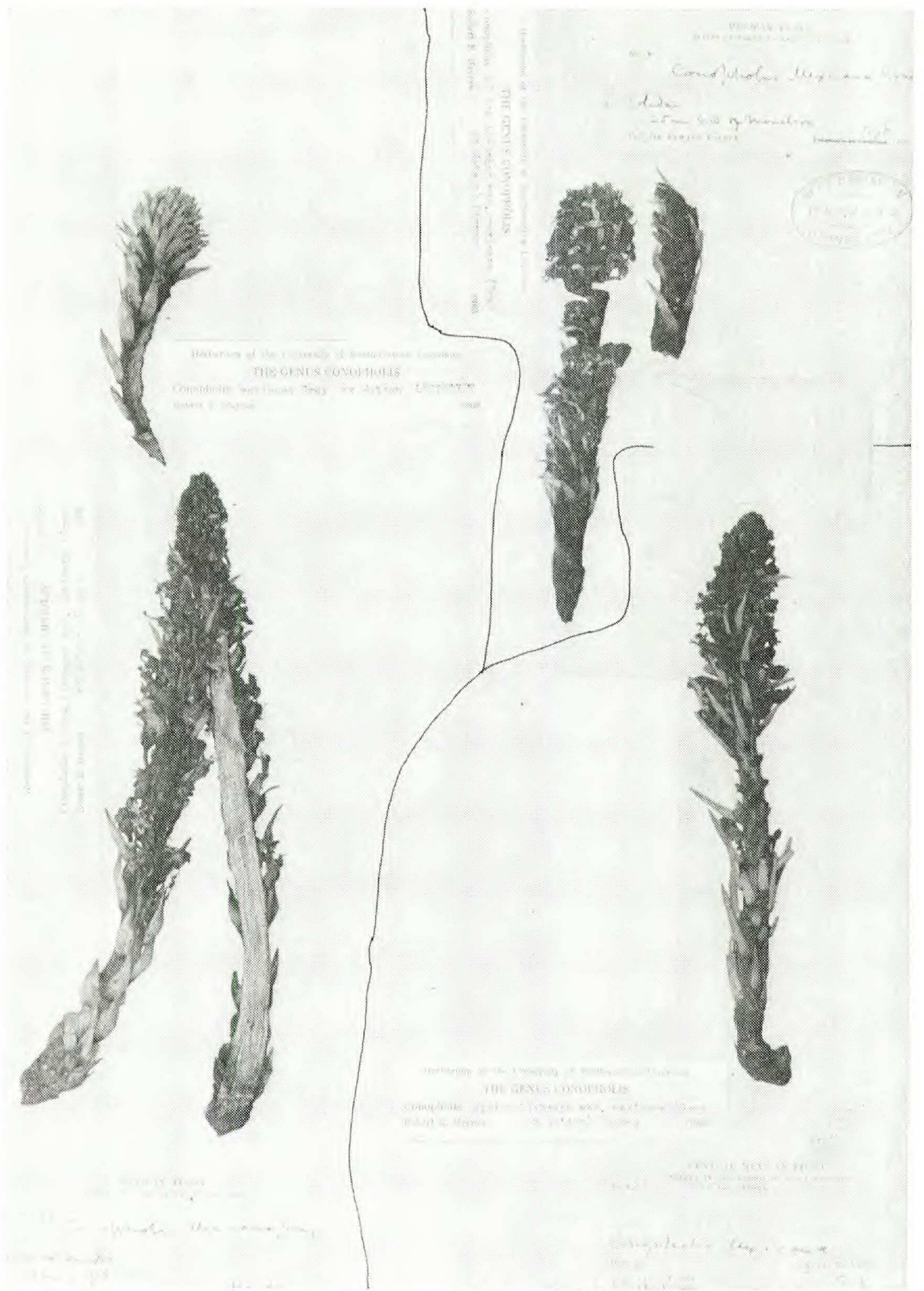


Fig. 8. *Conopholis alpina* var. *mexicana*. Photograph of holotype.